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The geological setting and palaeoenvironmental and palaeoecological reconstructions of the Upper Permian insect beds at Belmont, New South Wales, Australia

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ABSTRACT

The entomofauna of the Tatarian insect beds within the Newcastle Coal Measures at Belmont, north of Sydney, was described many years ago. A new collection contains some undescribed species, particularly beetles; a new exposure of the fossiliferous deposits is now documented. The Newcastle Coal Measures consist of sandstones, conglomerates, shales, coal and tuffs, which were deposited in the Hunter Trough. The depositional environment consisted of a series of very shallow, stagnant freshwater pools along a gravel river channel system within a regional coal swamp. A volcanic event produced a volcanic ash dump, causing a "snapshot" kill of insects, validating possible interpretation of percentages of insect fossils in ecological modelling. The pool community included Conchostraca, *Permosyne* beetles and extremely rare insect larvae. A community on swamp banks adjacent to the water courses was comprised of *Glossopteris*-dominated flora and *Phyllotheca*, with an insect-dominated, first-level consumer community of phloem-feeding Hemiptera and possibly pollenivorous Mecoptera. A leaf-litter and bark-dwelling community included Protelytroptera, Psocoptera and archostematan Coleoptera. Neuroptera, extremely rare Trichoptera, and ancestors of the Orthoptera were also present in small numbers. Adult Neuroptera fossils suggest the presence of their predatory larvae and this group, along with the Odonata, are considered to have been the predatory components within this environment. No chelicerates, tetrapods or other potential top predators have been found in this, or proximal, facies. Disruptive colour patterns in some of the insects may indicate predator-prey relationships. Of interest also is the identification of a number of *Glossopteris* leaves with chewed margins. If these observations are correct, they would represent one of the earliest records of this kind of ichnofossil in Australia.

KEY WORDS: Insects, assemblage, *Glossopteris*, *Phyllotheca*, palaeoreconstructions, swamp, taphonomy, volcanic ash.

INTRODUCTION

This paper is an attempt to interpret the palaeoenvironment of the Belmont area during the Upper Permian based upon the evidence of sedimentary structures and facies relationships of the beds underlying and overlying the Belmont insect beds. The paper gives some preliminary findings of the proportions of the various insect orders and discusses ecological implications.

Geological setting

The Belmont insect bed is found within the Upper Newcastle Coal Measures of New South Wales (Fig. 1). The Belmont insect bed consists of a thin chert seam which is located within the Belmont Conglomerate Member within the upper part of the Croudace Bay Formation. The Belmont insect bed varies in thickness from approximately 20 cm to a reported 800 cm. At all sampled sites, over an area of outcrop of approximately 20 km^2, the bed varies in thickness from 20 to 32 cm, with the most common thickness being 30 cm. The Croudace Bay Formation consists of sandstones, conglomerates, coal and minor volcanic chert and shales (Diessel & Moelle 1988). The Belmont Conglomerate

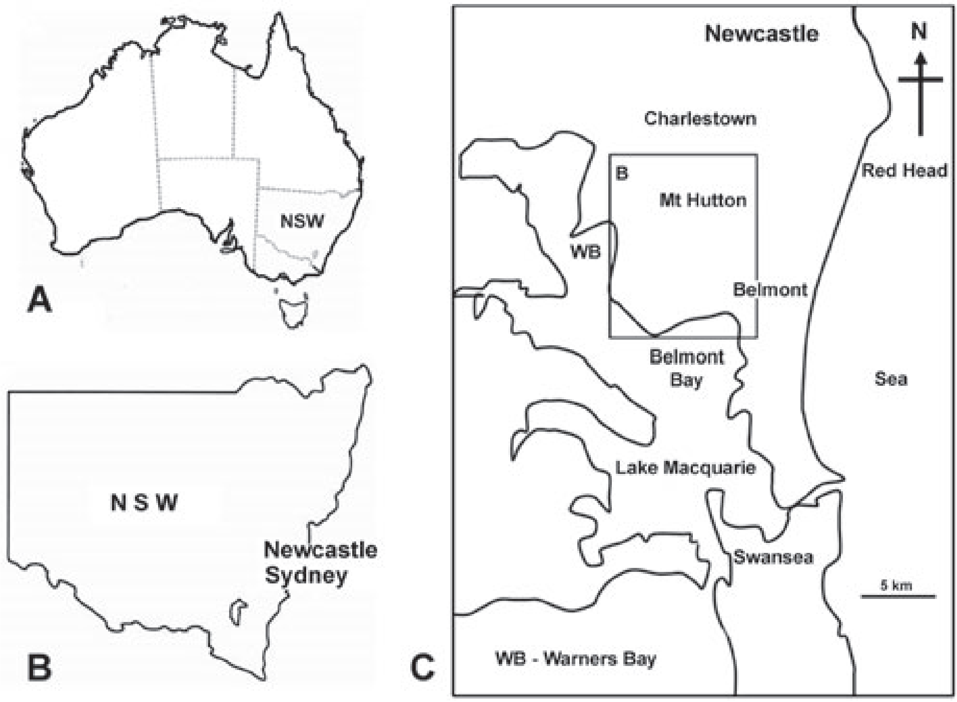

Fig. 1. (A) Outline map of Australia; (B) Outline map of New South Wales; (C) Map of Lake Macquarie area. The study area is enclosed in the rectangle.

filled an incised river valley and the stream, which deposited gravel within this valley, flowed in a south-southwest direction at approximately 210º (Herbert 1995). The gravel which filled the valley was sourced from the New England Fold Belt to the north-east (Little 1994), which was a highland region during the Permian. This river flowed into the Hunter Trough, which is part of the Sydney Basin, depositing gravel in the Belmont area, and sand further downstream, to the west, beyond Fennel Bay in the Lake Macquarie area (Engel 1966; Herbert 1995). The size of sediment grains decreased to the south-west (Brown *et al.* 1968). The Belmont Conglomerate is one of a number of lenticular fluvial bodies deposited during the Upper Permian in the Newcastle Coal Measures (Engel 1966). The volcano-clastic material deposited into the Newcastle Coal Measures during the Permian was sourced from volcanoes to the north or east (Wabrooke 1987). The Awaba Tuff and the Warner's Bay Tuff, above and below the Belmont Conglomerate respectively, thin out from north to south (Little *et al.* 1996). Marine sequences dominate the Early and Mid Permian of the Sydney Basin, but within the Upper Permian of the Newcastle Coal Measures the depositional palaeoenvironment grades upwards from beach-dominated coast and back-barrier swamps to braided plain, sheet-like alluvial fans and swamps. Coal-forming deposition proceeded throughout the Upper Permian of the Newcastle Coal Measures, which includes fourteen coal seams (Little *et al.* 1996; Wabrooke 1987) within a framework of transgression–regression cycles. Acritarchs have been found in strata immediately above the Croudace Bay Formation (Herbert 1995). The entire Newcastle Coalfield area was considered to be a high stand (Little *et*

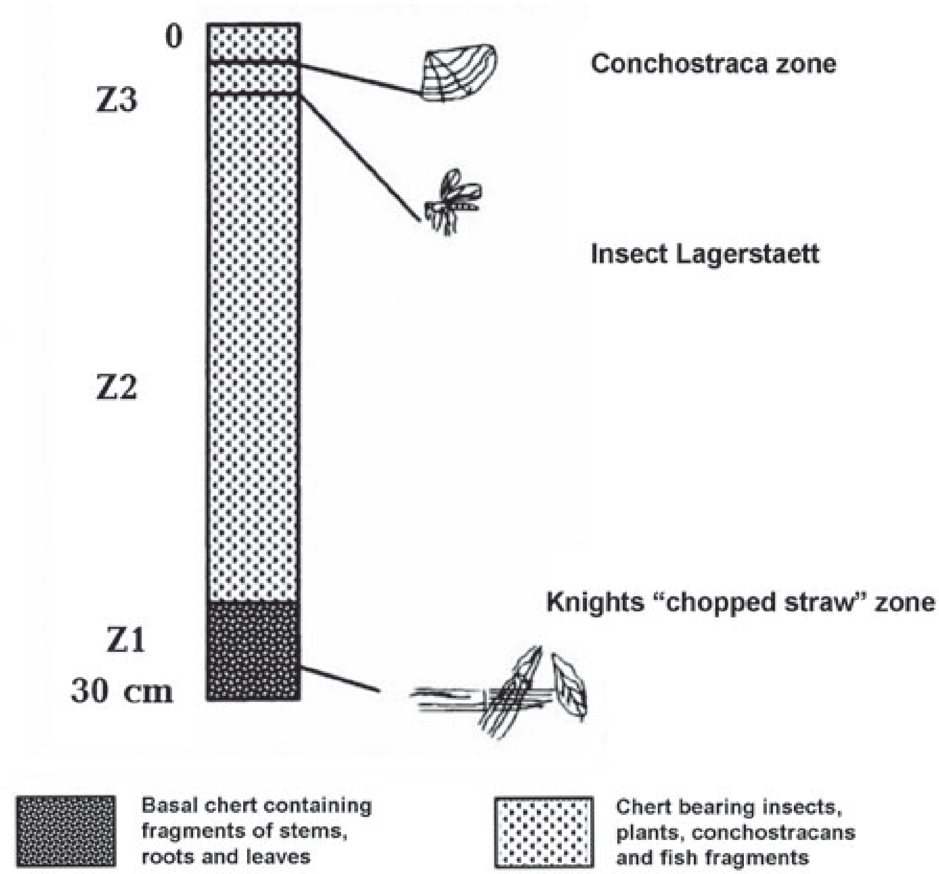
0
Z3
Z2
Z1
30 cm
Conchostraca zone
Insect Lagerstaett
Knights "chopped straw" zone
Basal chert containing fragments of stems, roots and leaves
Chert bearing insects, plants, conchostracans and fish fragments

Fig. 2. Section of insect seam from Pincombe's Outcrop (site 206, see Fig. 3).

al. 1996) during the Upper Permian. Herbert (1995) considered the depositional conditions of the Belmont Conglomerate to represent a low stand, within Sequence H, which was probably deposited between 253 and 251 million years ago (P. Jones, pers. comm.).

Depositional Environment

Geology of the Belmont insect bed

The Belmont insect bed consists of a lithified volcanic ash (chert) (Tillyard 1926), represented by a fine groundmass of devitrified glass shards and fine phenocrysts, mainly consisting of feldspars, in addition to some opaque material. In thin section, the grains show linear alignment, and in sliced, insect seam blocks, fine horizontal bedding planes are visible. No cross-lamination has been observed. There is slight upward fining within the insect seam, more obvious in some specimens than others. The seam dips gently to the west and weathers to generally rhomboidal blocks. At most localities it has three distinct vertical zones. A section of insect bed from site 206 (Fig. 2) is typical of the sequence at all sites sampled along the Violet Town Ridge. At other sites there are variations in the presence and thickness of a Conchostraca layer, in the zonation of the fossil insects and in the presence or absence of a basal layer known as the "chopped straw" zone (Knight 1950).

Zone 1. This is the lowest zone, and, where present, it consists of chert with a distinct appearance. It is grey, has a slightly coarser texture than the zones above it and has a fine groundmass with distinctly larger phenocrysts, which are generally linearly aligned. It also contains a large and instantly recognisable component of fossil phytobioclastic remains. This consists of highly fragmented stem sections of *Phyllotheca*, leaves of *Glossopteris* and sections of *Vertebraria* (roots of *Glossopteris*). These remains are chaotic and non-aligned. In general, Zone 1 is approximately 5 cm thick. Cut sections reveal no evidence of flow structures.

Zone 2. This zone has a slightly finer groundmass than that of Zone 1 and phenocrysts are much the same size as in the groundmass. The mineral composition of this zone appears to be the same as Zone 1. There is no fragmentary fossil plant component, except for occasional, isolated and very well-preserved *Glossopteris* leaves, becoming marginally more common towards the top of the zone. Zone 2 also contains very rare fossil insects and Conchostraca and is approximately 20 cm thick.

Zone 3. This is the uppermost zone. In the lowest layers it contains numerous well- to poorly-preserved *Glossopteris* leaves, seeds, fructifications, blackened carbonaceous leaf scraps and occasional *Phyllotheca* stems, usually found in unpredictable layers. Above it, there is a distinct insect-bearing layer, which also commonly contains well-preserved plant material, particularly *Glossopteris* leaves and less common fructifications, as well as Conchostraca, rare fish scales, fish scale clusters and a number of fish fins. The *Glossopteris* leaves are often complete, though sometimes crumpled. The layer varies from pale grey to yellow-white, and is often blotchy. Immediately above the insect layer, there is a Conchostraca (*Leaia*) layer, which contains abundant and easily-identifiable valves, both isolated and paired. In some rock slabs, the valves of Conchostraca are clustered. There are also occasional insect fossils embedded within this layer. Immediately above the Conchostraca layer, the chert is grey-white, blotchy and generally too weathered to reveal fossil content. Zone 3 is approximately 4 cm thick. At several sites, the non-ribbed conchostracan *Estheria* is found as well as *Leaia*. The Belmont insect bed outcrops in the Belmont area, north-west in the Kimbles Hill-Mount Hutton area, and to the west along the eastern shore of Lake Macquarie (Fig. 3).

Underlying Seam

The Belmont Conglomerate is widespread over the Belmont area and is exposed at various accessible sites including Brown's Outcrop, Burton Road, Croudace Quarry, 205, 206, and St Andrews Park (Fig. 3). This is a 41 m thick seam (Herbert 1995), with the thin insect bed being located near its middle part. Various facies ranging in thickness from 2 m to approximately 5 m occur between the top of the conglomerate underlying the insect bed and the base of the insect bed itself. These facies include coal, shale and fine sandstones, often in varied combinations at different sites. At most sites, weathered shale forms a layer directly beneath the insect seam. Fossil plant material within this shale is poorly preserved due to weathering. Coal has not been observed in direct contact with the base of the insect bed at any observed site. At one site (LCl, Fig. 3), sandstone is in direct contact with the insect bed.

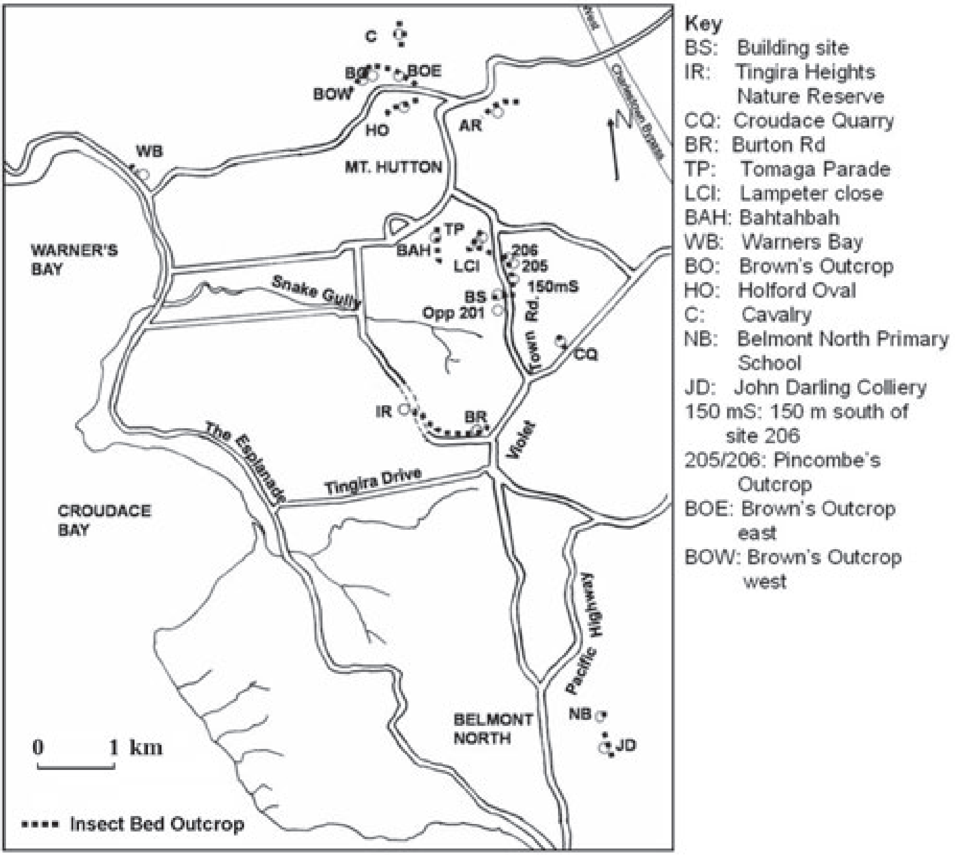
C
BO
BOE
BOW
HO
AR
WB
MT. HUTTON
WARNER'S BAY
TP
BAH
LCI
206
205
150mS
BS
Opp 201
Snake Gully
Town Rd.
CQ
IR
BR
Violet
The Esplanade
Tingira Drive
CROUDACE BAY
Pacific Highway
BELMONT NORTH
NB
JD
Charlestown Bypass
N
0 1 km
Insect Bed Outcrop
Key
BS: Building site
IR: Tingira Heights Nature Reserve
CQ: Croudace Quarry
BR: Burton Rd
TP: Tomaga Parade
LCI: Lampeter close
BAH: Bahtahbah
WB: Warners Bay
BO: Brown's Outcrop
HO: Holford Oval
C: Cavalry
NB: Belmont North Primary School
JD: John Darling Colliery
150 mS: 150 m south of site 206
205/206: Pincombe's Outcrop
BOE: Brown's Outcrop east
BOW: Brown's Outcrop west

Fig. 3. Map of Belmont insect beds, showing new and old collection sites.

Overlying Seam

The rock in contact with the top of the insect bed is a fine sandstone and, where a section is exposed, this sandstone continues for at least 5 m, or there are alternate sandstone and conglomerate sequences (e.g., Brown's Outcrop), where the overlying seam is exposed vertically over approximately 30 m. A minor, discontinuous layer of shale exists within this overlying sequence at Brown's Outcrop.

MATERIAL

The author took great care to collect both parts and counterparts (when possible) for a new collection for the Australian Museum (approximately 800 specimens or 400 insects), and to collect and record as much data as possible for this study. The Richard Brown collection (Australian Museum) consists of approximately 80 specimens. The Australian Museum collection of fossil insects from Belmont consists of approximately 1500 specimens. Many counterparts are indicated, but it is unclear how many individual insects are actually in the collection. The original collectors donated specimens sporadically so that numbers of donated parts/counterparts may be quite different and the relationship not recognised at registration. The Natural History Museum (London) collection consists of approximately 1000 specimens (A. Ross, pers. comm.), but the ratio of parts and counterparts is unknown at present.

TAPHONOMIC EXPERIMENT

A taphonomic experiment was conducted to observe the effect of a simulated volcanic ash shower on insect remains floating on an astatic water surface, in an attempt to find a mechanism to explain why some fossil insect wings are found below the Lagerstätten at the top of the Belmont insect bed. A one-litre jar was set up and partly filled with water. Insects were collected and sprinkled on the water surface. All the insects floated. A fine metal sieve was set up on the mouth of the jar. Gentle continuous dumping of a denatured cement powder into the container commenced in order to simulate an ash dump. Zones 2 and 3, of the Belmont insect bed, appear to have been formed by gentle, vertical ash accumulation. The majority of the experimental insects remained floating, despite this process of "ash" loading. Two insects submerged partially, and others actually sank to the sediment-water interface near the base of the container. This experiment may explain the mechanism by which insect remains are distributed. The mechanism appears to involve both increased ash load on floating insect parts, and the upward capillarity by water at the water-air interface on the "ash" load. Through saturation of pore spaces, the ash load becomes heavier, adhering to the insect remains which causes them to sink. If this is the case, then the majority of insects at Belmont insect beds have accumulated as a wing-float Lagerstätt, and the remainder have sunk and accumulated lower in the seam as a result of ash-loading.

PALAEOENVIRONMENTAL INTERPRETATION

Physical environmental evidence

The geometry and lithology of the Belmont Conglomerate is indicative of a major, upper-flow regime river channel, or channel system, grading into a lower-flow regime with a fining of facies further downstream (Brown *et al.* 1968). The Belmont area itself represents the braided channel part of this system, and the sandstone facies further south represent the delta-fan part of the system. Facies between the conglomerate and the base of the insect seam (coals, fine sandstones and shales) suggest an accumulation of overbank sediments adjacent to the river channel system, or possibly overbank sediments within the channel system itself. Overbank deposits of this type would be the result of overflow during flood times, in which the fines would accumulate on the bottoms of the ponds. Alternatively, these silty sediments could represent cessation of flow in the main channel system for an indeterminate time prior to the volcano-clastic deposition of the insect tuff layer. They may also indicate channel migration. Dunbar and Rogers (1957) found that thick sedimentary deposits are now forming at the foot of many of the mountain ranges in the United States, and that these alluvial fan deposits tend to have multiple channels with bedding approximately parallel to the fan surface, and with cross-stratification down fan in each channel and imbricated pebbles upfan. These characters are similar to those observed in the Belmont Conglomerate. Furthermore, Dunbar and Rogers (1957) found that such channel systems build up natural levees between them. It is likely that there were one or more channels, with island and fringing levees within the channel system of the Belmont Conglomerate. Where abandoned channels connect with active channels, traps for silt and other fine-grained sediments can form, which create shoestring geometries corresponding with the original channel forms (Selley 1972). Deltaic floodplain has a significant proportion of silt-sized sediment (Folk 1968). Accumulations of this sediment therefore indicate low or no flow conditions as are commonly found in overbank ponds.

No autochthonous plant remains have been identified *in situ* in the decomposed shales directly underlying the insect seam, thus it is likely that trees were unable to establish in the overbank ponds because of water logging and poor aeration of roots. Evidence of Conchostraca (discussed below) also suggests that these overbank ponds were ephemeral. However, adjacent coal facies indicate co-existence with peat swamps which generated the coal deposits of the Newcastle Coal Measures and provide the abundance of fossil *Glossopteris* leaves, fructifications and some suspected autochthonous insects within the insect seam. The insect seam is thin, approximately 30 cm, apparently continuous and spatially widespread within the study area, notwithstanding general erosion of the area to ridges. This suggests that an isochronous “single dump” of volcanic ash resulted in the formation of the insect bed. Cut sections of blocks from the insect seam have no flow indicators such as cross lamination, or obvious sole marks along parting planes. This suggests that the ash was deposited in horizontal layers in non-flowing pools. The most likely model would be that the pools were either remnants of a drying main channel system, or overbank pools situated between the main channel system and the coal swamps. Zone 1 seems to grade abruptly into Zone 2, while Zone 2 seems to grade into Zone 3 without a clear break, giving the distinct appearance that the entire insect bed was deposited as a continuous process, which started with the sub-aerial dumping of shattered *Phyllotheca* stems from a directed volcanic blast, or from a lahar, followed by vertical deposition of ash and insect parts from the attendant ash cloud.

A possible sequence of events during formation of the Belmont insect beds is represented in Fig. 4. Stage 1 of the volcanic event is a directed blast (represented by the large horizontal arrow). This event shattered *Phyllotheca* thickets and carried debris, perhaps as a lahar, which settled into the bottom of overbank ponds in the D area of the diagram, to form layer C. In stage 2, volcanic dust from the attendant ash cloud (F) was steadily deposited onto the surface of the shallow overbank ponds. This filled up the ponds with volcanic mud E. During the process, conchostracans were forced to the surface, forming a layer, where they subsequently died. Insect remains were also deposited from the ash cloud onto the surface of the ponds D, where wings accumulated until they became incorporated into the wet volcanic mud. Other insect remains, and *Glossopteris* leaves were deposited from the swamp banks.

Fossil environmental evidence

The presence of fossil insects with aquatic immatures, such as *Nannochorista* (Mecoptera), and particularly of insects favouring cold, clear, pure, flowing water (Plecoptera) is strong evidence for a cold, lotic, depositional environment at Belmont (Tillyard 1935*b*). At the same time, there is contradictory fossil evidence of a Conchostraca bloom, in the form of highly abundant carapaces in the insect seam at almost all sampled sites. Modern Conchostraca generally live in ephemeral pools (Webb 1979; De Deckker, pers. comm.), which suggests low or absent water flow. It seems

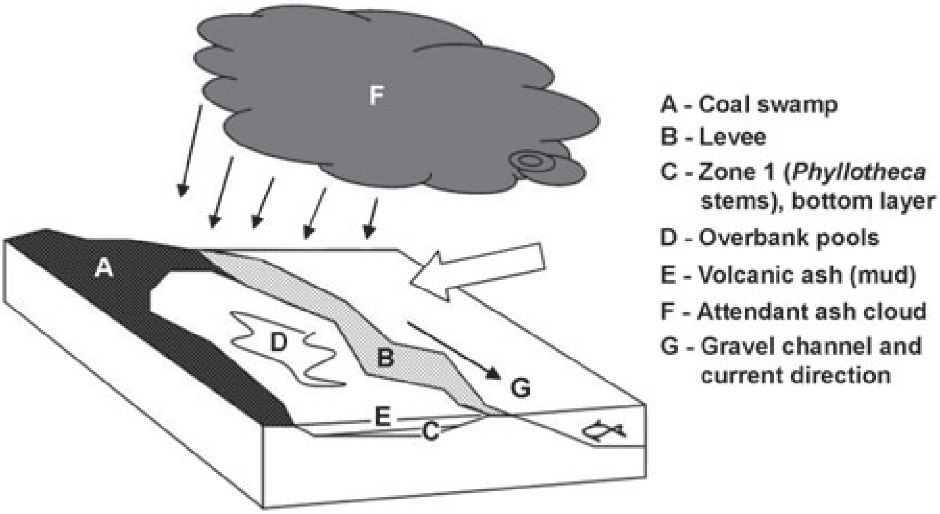

Fig. 4. A block model of the Belmont coal swamps and gravel channel system.

possible that before the tuff dump, a normally high-energy, gravel-depositing, perennial system stagnated for some time. Spillage into overbank pools ceased, and both the evaporation of, and seepage from, the pools triggered a Conchostraca bloom. If this is correct, then the Plecoptera larvae were either remnant entomofauna in the pools, or were washed into the pools by overbank spill from the main channel system prior to, or during the ash dump, as a result of storms which may have been associated with the volcanic event.

The abdomen of a Plecoptera nymph was found by Pincombe (Tillyard 1935*b*) and very recently, both a complete and partial Plecoptera nymph were found near Belmont by T. Annable (pers. comm.) in a fine sandstone within the Belmont Conglomerate at a horizon slightly above the Belmont insect bed. Occasional fish remains have also been found in the insect seam, including rare scales and even rarer fin parts. It is likely that fish might have been relocated from the main river channel into ephemeral pools during a flood or high flow prior to the ash event, became stranded and then died as the pools evaporated, stagnated and possibly became anoxic. Under these circumstances, the fish would have decomposed and disarticulated, becoming fossil components with the conchostracans and insects. At most sites, both conchostracans and insects are distinctly zoned, and fish remains, where recovered, are invariably found within the same upper part of the bed.

A possible mechanism explaining the distribution of Conchostraca in the insect bed can be suggested. After initial emplacement of disarticulated *Phyllotheca* stem sections, resulting from either a directed blast or a lahar mud wash, the volcanic ash fell as a continuous shower into shallow pools at least until the pools were filled. As the water became shallower, the Conchostraca were forced upwards until they became stranded in the evaporating pools. Conchostraca usually inhabit the bottom area of ponds (P. Jones, pers. comm.), but in this case, vast numbers were exposed to the effects of desiccation and perhaps heat and noxious volcanic gases, resulting in their death. The retrieval of clumped fossil specimens may be indicative of this event. The fossil insects appear to be both allochthonous, presumably dumped out of attendant dust clouds from a volcano to the east, and autochthonous, from the leaf litter and foliage associated with adjacent swamp banks, and from the pools themselves.

Seasonal implications

Glossopteris leaves and fructifications are very abundant as the main plant fossils in the insect bed. *Glossopteris* leaf fossil accumulations suggest that this tree was deciduous (White 1998) and thus it is possible that the ash dump and insect seam formation occurred during autumn. However, it is also possible that the accumulation of leaves was caused by volcanic blasts, and therefore is not necessarily indicative of a season.

Allochthonous insect remains

Isolated wings constitute the bulk of insect remains (approximately 95% of insect fauna). It is probable that the majority of the wings were from insects which had suffered exposure to volcanic activity. If these insects were transported from between the volcanic source and the deposition site, then a winnowing effect probably caused a negative bias against body parts, and a positive bias in favour of wings. These wings were probably derived from insects further upstream and are assumed to be part of the same swamp/channel ecosystem (Fig. 5).

There are a number of insect remains of complete and partially complete specimens (approximately 5% of insect fauna). These are likely to have originated from two sources; from the swamp banks beside the ponds and from the ponds themselves. The majority of complete to semi-complete specimens are psyllids, a few psocids and beetles. The psyllids and psocids are likely to have inhabited the swamp banks, infesting the trees and shrubs; the Protelytroptera and grylloblattids probably inhabited the leaf litter, occupying the same niche as cockroaches today. Archostematan beetles probably inhabited rotting tree trunks, while *Permosyne* beetles inhabited the water surface and body of the pools. However, interestingly, there are other insects which might have been (at least partially) autochthonous, particularly the Mecoptera, which probably fed on the pollen provided by the abundant fruiting bodies and detritus. The less common Neuroptera would have preyed upon the abundant, sap-sucking Homoptera.

In terms of insect preservation, there appears to be an obvious bias toward smaller insects, i.e. the smaller the insect, the more likely it is to be preserved intact. Curiously, although there is a bias against large wings, the (often) large Protelytroptera wings are, almost without exception, completely well-preserved. There is little doubt that this is due to the toughening of the fore-wings in the form of elytra, but no other body parts have ever been found associated with these elytra. This is most surprising, since these insects probably lived in the leaf litter along the banks adjacent to the pools, and thus may not have been subjected to the full effect of volcanic activity experienced by the Mecoptera, Neuroptera and Odonata adults. The apterous immatures of Hemiptera are likely to have been present in significant numbers, inhabiting trees and shrubs; and yet few fossils of these immatures, relative to the abundance of preserved adult wings, have been found. A reason for this may be that wings of adults were more easily dumped into the pools from the banks than apterous immatures. Selected fossil insects from the Belmont insect beds are illustrated in Fig. 6.

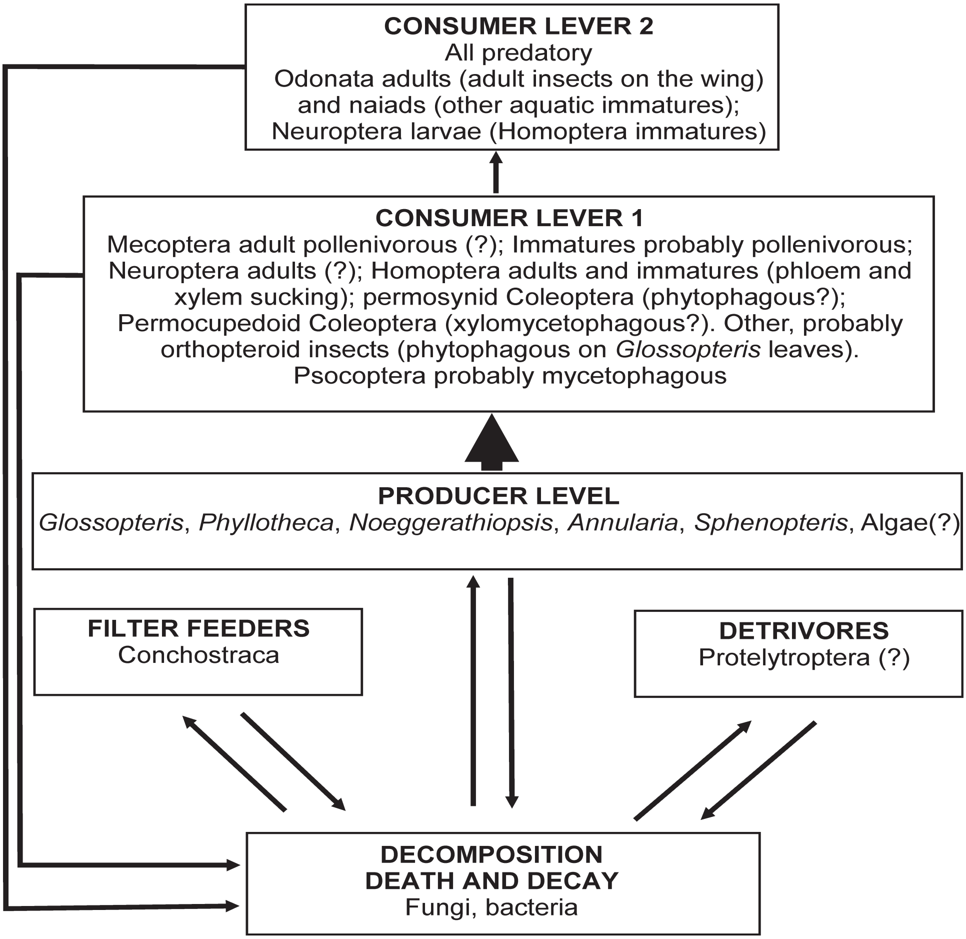
CONSUMER LEVER 2
All predatory
Odonata adults (adult insects on the wing)
and naiads (other aquatic immatures);
Neuroptera larvae (Homoptera immatures)
CONSUMER LEVER 1
Mecoptera adult pollenivorous (?); Immatures probably pollenivorous;
Neuroptera adults (?); Homoptera adults and immatures (phloem and
xylem sucking); permosynid Coleoptera (phytophagous?);
Permocupedoid Coleoptera (xylomycetophagous?). Other, probably
orthopteroid insects (phytophagous on *Glossopteris* leaves).
Psocoptera probably mycetophagous
PRODUCER LEVEL
Glossopteris, *Phyllotheca*, *Noeggerathiopsis*, *Annularia*, *Sphenopteris*, Algae(?)
FILTER FEEDERS
Conchostraca
DETRIVORES
Protelytroptera (?)
DECOMPOSITION
DEATH AND DECAY
Fungi, bacteria

Fig. 5. An attempted reconstruction of the ecosystem of the Belmont coal swamp and overbank pools. The main component insect groups, conchostracans and plants preserved in the oryctocoenosis are illustrated here and assigned to definite, probable and possible feeding groups.

There is no evidence of *Glossopteris* tree trunks within the insect bed, apart from a few fossilised twigs, possibly from *Glossopteris* trees.

Palaeoflora

The preserved flora appears to be of low diversity, consisting primarily of the peltasperms *Glossopteris* and *Gangamopteris* and the sphenopsids *Phyllotheca* and *Annularia*. *Noeggerathiopsis* and *Sphenopteris* are also present. As mentioned above, the abundance of *Glossopteris* leaves might have been due to autumn fall. This means that *Glossopteris* may be overrepresented in the oryctocoenosis compared to *Phyllotheca*, which is most commonly represented by fossil specimens of stem sections rather than leaves. Their leaves are inconspicuous, generally highly fragmented, hard to quantify, and as a result may be underrepresented in the compositional analysis.

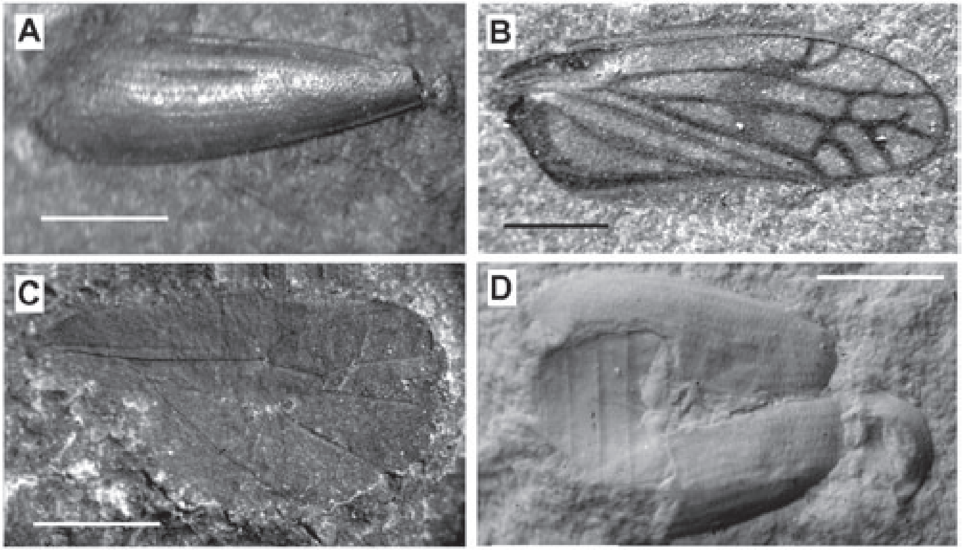

Fig. 6. Fossil insects: (A) *Permosyne pincombeae* (Coleoptera), holotype, Australian Museum AM F 19778 (original no. 14 T), note the indent, indicating the presence of a schiza, an adaptation to life in the water; (B) Wing belonging to an insect closely related to *Stenoviicia incerta* (Homoptera), specimen no. AM F 12948 (original no. B 325); (C) Wing of an undescribed protopsyllid (?) (Homoptera), specimen no. B 87; (D) *Permosyne mitchelli* (Coleoptera), specimen no. AM F 41273 (original number K129). Scale bars = 1 mm.

The peltasperms and sphenopsids form the primary producer basis for the Belmont ecosystem. Tillyard (1936) did not believe that sphenopsids were a food source for insects: "...nobody would accuse an insect with having anything to do with the Equisetales." However, there may have been a feeding association between flightless nymphs of an undescribed paraknightid (Hemiptera) and *Phyllotheca* in Permian strata in Siberia (Zherikhin 2002) and paraknightids are known from the Belmont region. Tillyard (1936) also identified what he considered to be a true choristid at Belmont and believed that this provided evidence of pollen eaters within the fossil insect fauna. The most likely food sources provided for insects by *Glossopteris* would have been phloem juices of the vascular tissue and the male fructifications, which would have provided pollen. There is also a possibility that these plants provided sugary rewards such as pollination drops, nectaries on vegetative tissues, and honeydew (see Labandeira 2002). Some insects may also have been folivorous, since chewed *Glossopteris* leaves have been found in the Belmont insect seam, and there is evidence of probable oviposition in the cambium tissue of *Phyllotheca* (Fig. 7B).

Disruptive colour patterns

A number of wings demonstrate chequered patterns while others show disruptive patterns. Such patterns have been observed in Mecoptera, Homoptera and Neuroptera. This may indicate predator or prey adaptations for camouflage within the dim and mottled light conditions of the coal swamps.

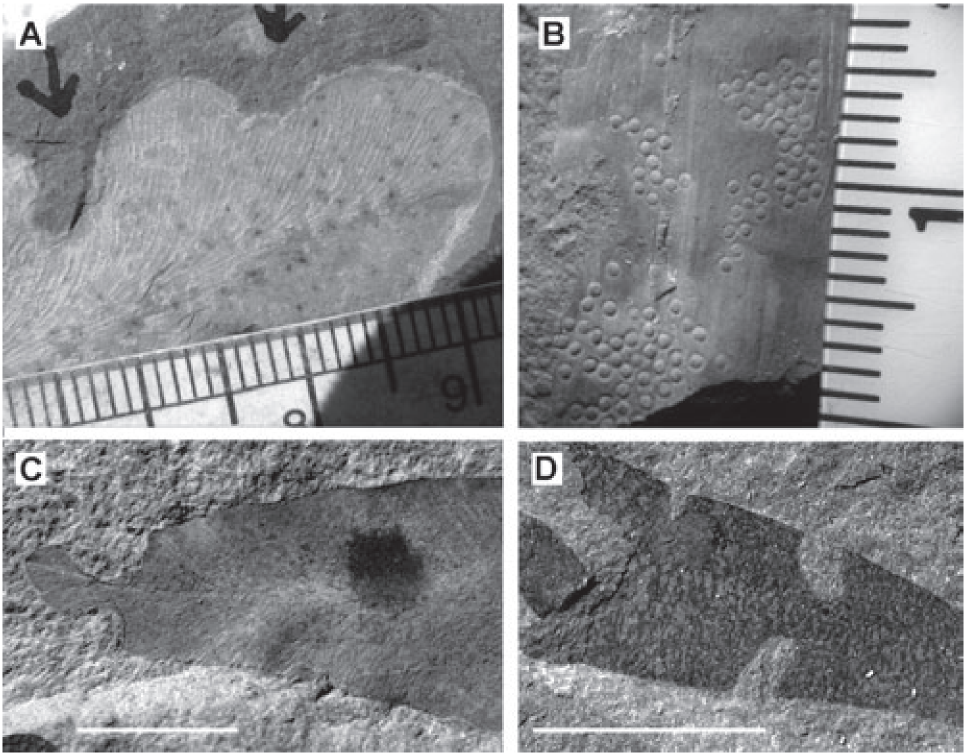

Fig. 7. Ichnofossils: (A) Chewed *Glossopteris* leaf margin, specimen BPl 3; (B) Probable insect eggs oviposited into a *Phyllotheca* stem, specimen AM F 122931; (C, D) Chewed *Glossopteris* leaf margins, specimens BPl 1 and BPl 2. Scale bars = 1 mm in Figs A, B and 1 cm in Figs C, D.

Plant–insect interactions

A number of chewed *Glossopteris* leaves and other presumed plant palaeopathological effects have been discovered very recently at Belmont during the collection of fossil insects. Specimens BPl 1 and BPl 2 (Figs 7C, 7D) are both discontinuous marginal chews and both are close to the apex of the pinnule. A number of other unnumbered specimens represent continuous chews along the pinnule margin (Fig. 7A). One specimen has been found in the Australian Museum collection on the “unidentified” Belmont fossil insect shelves, which consists of a small fragment of *Phyllotheca* stem, with embedded insect eggs.

PALAEOECOLOGY

Because elements within this ecosystem were most probably preserved as a result of a “snapshot” event, and the oryctocoenosis is similar to a thanatocoenosis, it seems reasonable to compare percentages of insect remains from different groups in terms of dietary guilds. This is further based upon the assumption that each single wing represents an individual insect (except, for example, where associated remains make it obvious that one individual is involved).

Percentage analysis was done based on the new collection (B collection). There is no obvious way of estimating biomasses involved at Belmont. However, ecological inter-

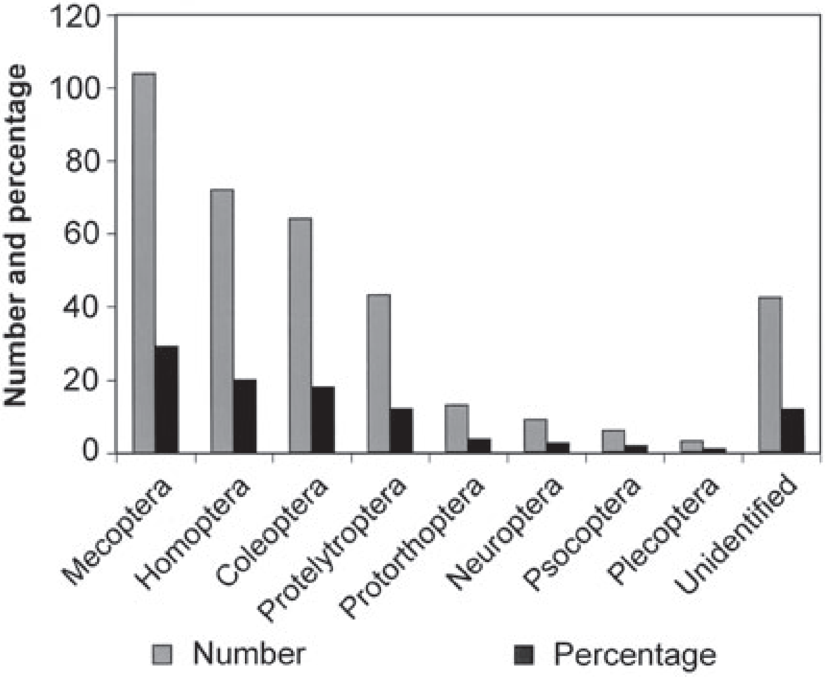

Fig. 8. Analysis of insect orders by number and percentage of individual insects (not total specimen numbers), Belmont insect beds, based upon new Beattie collection (2002–2004).

actions are suggested below, in order to illustrate feeding relationships. The most obvious insect predator–prey relationship in this ecosystem is that between neuropteran and homopteran immatures. No Neuroptera larvae were found but the remains of the adults of both orders indicate the presence of immatures within the biocoenosis and a few specimens of fossilised immature Homoptera exist in the Australian Museum collection. There are very few fossil remains of Odonata, but it would seem probable that these insects preyed upon flying insects such as the abundant Mecoptera. In this study, it is recognised that feeding behaviour in some of the fossil insect groups present at Belmont is unknown.

Four orders dominate the insect biocoenosis in the Belmont coal swamps and channel system, the Mecoptera, Homoptera, Coleoptera and Protelytroptera. Although subject to biases (as mentioned above), these data represent an approximation of the insect biocoenosis (Fig. 8).

The dominant Mecoptera family at Belmont was the Permochoristidae and the most abundant species was *Mesochorista australica*. Assuming the possibility that the direct ancestors of the Choristidae were the permochoristids, it is reasonable to consider that the two occupy a similar feeding niche. However, doubt has been shed on the relationships of extant Mecoptera to those of the Permian (D. Shcherbakov, pers. comm.). Tillyard (1922) believed the Permochoristidae to be pollenivorous, or an type of primary consumer, feeding on the abundant male reproductive bodies of *Glossopteris*, which are found as fossils in this seam, or dispersed pollen. Tillyard also believed that most of

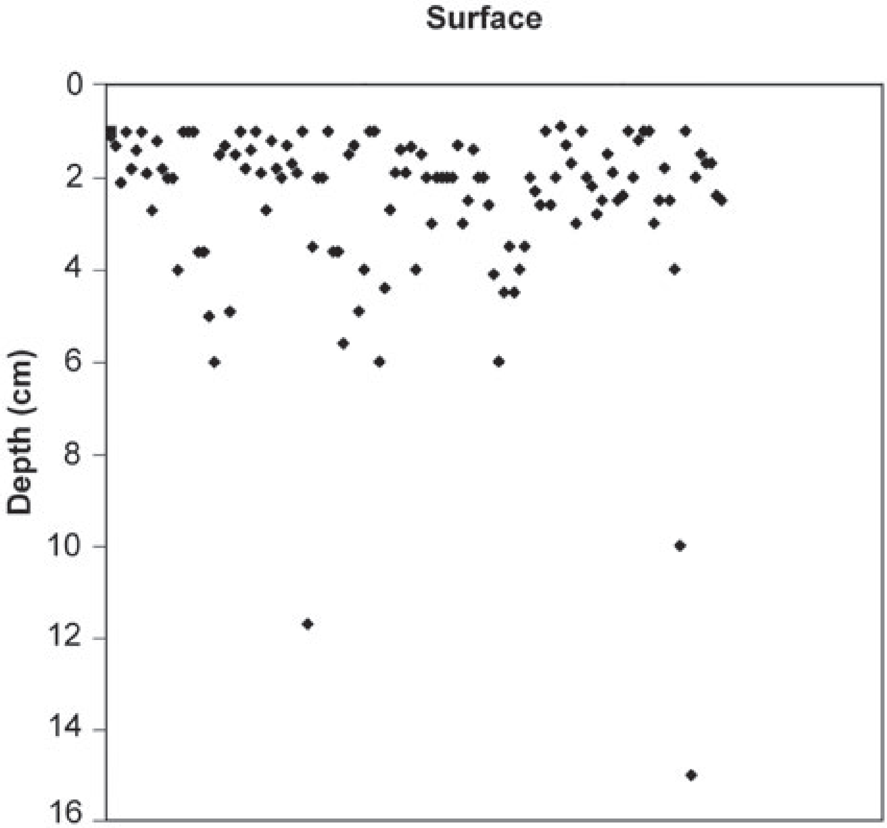

Fig. 9. Depth of fossil insects at site 205. Most wings are found in a Lagerstätt at a depth of 2 cm within the seam.

the other scorpionflies (and the Neuroptera) fed on the Hemiptera and Diptera, and considered the primitive scorpionflies to have possibly taken the place of the cockroaches (Tillyard 1922), which would make them detrivorous. The larvae of the *Nannochorista* (Mecoptera) possibly developed in pools and also fed on pollen banks in the leaf litter beneath the canopy (Strong *et al.* 1984).

The Homoptera are also significant primary consumers since Homoptera are regarded as phloem-feeders with highly specialised mouthparts for this purpose (Shcherbakov 2000), and some are xylem feeders. The plant community appears to have been largely bispecific, consisting primarily of *Glossopteris* and *Phyllotheca*, and thus it is likely that the Homoptera extracted the juices of these two plants.

In terms of the Coleoptera, high proportions of permosynids, *Permosyne belmontensis*, *P. mitchelli* and *P. affinus*, have been observed, with the most common being *P. belmontensis* and *P. mitchelli*. *Permosyne pincombeae* was also fairly common; the species has been transferred to the Rhomocoleidae (Ponomarenko 2003). *P. pincombeae* specimens have a distinct elytral groove not mentioned in Tillyard's original type description. This indicates a device for trapping an air bubble below the elytra for an aquatic mode of life (Ponomarenko 2002). Other beetles appear to belong to the families

Permocupedidae, Asiocoleidae, Taldycupidae and Schizocoleidae (Ponomarenko, pers. comm.), and the first three of these other families were bark beetles.

The Lophioneuridae probably fed on pollen and lived in the pollen sacs of host plants (Strong *et al.* 1984) while the Protelytroptera were the main scavengers of the leaf litter along the spongy swamp banks (assuming feeding habits were similar to that of their dermapterous descendants). Neuropteran immatures almost certainly preyed on homopteran immatures (Tillyard 1922). The Psocoptera probably grazed on fungi growing on tree and shrub trunks in this cold, damp environment. Modern grylloblattids, known as ice crawlers, feed on dying and immobilised insects. If there is an ancestral relationship, then there is a possibility that some of the fragmentary and poorly known grylloblattid fossils from Belmont had similar feeding habits, although they are the main suspects for folivory of *Glossopteris* in a Gondwanan flora of Brazil (Adami-Rodrigues *et al.* 2004).

CONCLUSIONS

The pre-eruptive environment during the Tatarian in the Belmont area consisted of the upper delta tract of a gravel channel system flowing through and within a regional coal swamp. A series of overbank ephemeral pools existed and probably periodically filled and then dried out over a number of years, building up layers of silty mud and sand of varying thicknesses. Prior to the volcanic event which resulted in the formation of the insect seam, a Conchostraca bloom had developed as the pools shallowed and started to dry out. A community of water beetles co-habited with the conchostracans. Fish trapped in these pools had died, possibly due to anoxia, and were in a state of advanced decomposition. Swamp banks beside the ponds were lined with *Phyllotheca*, *Glossopteris, Gangamopteris*, less common *Noeggerathiopsis* and rare *Sphenopteris* and *Annularia* plants. *Glossopteris* and *Gangamopteris* had lost the bulk of their leaves as a result of either seasonal change, or, more likely, by volcanic blast. Because Belmont was within Gondwanaland at a palaeolatitude of approximately 80º S, the ambient temperature was very low. A community of swamp insects existed based upon primary production by the swamp plants. A single volcanoclastic event occurred, depositing a blanket layer of tuff over the swamps and filling the shallow, ephemeral pools. The volcanic ash fall may have been uneven, resulting in thickness variation at particular sites. This event was energetic enough to deposit a layer of fragmented *Phyllotheca* stems and either the directed blast or a pyroclastic flow killed and disarticulated a large number of insects, which over time, fossilised within the ash-filled ponds. Homoptera and Mecoptera are the orders which are found to be most abundant at Belmont. It is almost certain that the Homoptera were primary consumers of plant phloem, and the Mecoptera (*Permochorista*) were primary consumers of pollen and also detrivores. The feeding niche of different groups of Coleoptera, including the rare bark beetles and probably the water beetles, was most likely that of xylomycetophagy and zoophagy, which would place them as secondary consumers. Of the identifiable higher-level consumers, the only definite examples are the Neuroptera and their immatures, which form a minor component of the fauna, in addition to the extremely rare Odonata. Other insect groups seem to have been involved in detrivorous and mycetophagous activities, associated with recycling, except for the rare Grylloblattida, which may have been, at least partly, folivorous. Fossil tetrapods have been found in strata much lower than at

Belmont in the Newcastle region (Warren 1997). Thus it is possible that these were the top predators within the ecosystem at Belmont.

In the final stages, river flow resumed along the channel system and the widespread deposition of sand, which encapsulated the tuff muds of the overbank ponds, allowed diagenetic processes to commence, resulting in lithification, and the preservation of the insect seam within the Belmont Conglomerate Member.

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